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The Origin of Asplenium ebenoides

BY MARGARET SLOSSON

The question whether *Asplenium ebenoides* R. R. Scott is or is not a hybrid between *Asplenium platyneuron* (L.) Oakes and *Camptosorus rhizophyllus* (L.) Link has long been a vexed one. In order to ascertain the truth by crossing *A. platyneuron* and *C. rhizophyllus*, I began experiments several years ago which had been suggested by Mr. George E. Davenport.* Partial description of these experiments, together with a discussion of the advantages and disadvantages of various methods of attempting the hybridizing of ferns, has been announced already, † but it is necessary to refer here to the method that Mr. Davenport suggested and which, with slight modification, was at first adopted.

This method consists of dividing prothalli of two species between the archegonial and antheridial regions before fertilization has taken place and planting the archegonial section of a prothallus of one of the species close to the antheridial section of a prothallus of the other, so that antheridia and archegonia come in contact. The idea is that should fertilization subsequently take place it can only be cross-fertilization and the resultant plant a hybrid. It should be said that although the formation of plants of pure species from asexual growth, which sometimes occurs on prothalli, would not be prevented, yet plants arising in this way can be distinguished, according to Dr. Farlow, from plants springing from fertilized archegonia and can, therefore, be detected and removed.

On experimenting, however, two objections to this method were encountered: (1) Nearly all of the sections of prothalli

* Papers Pres. Boston Meet. (1898), 9. 1899.

† Fernwort Papers (ined.).

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sent out branches and it appeared extremely probable that on the branches the organs that had been removed were often regenerated. Each of the branches was shaped more or less like a complete prothallus, and many produced plants of pure species borne, as in the normal prothalli, close to a sinus. I did not wish to disturb the cultures sufficiently to make certain, but it is not probable that all, if any, of these plants were the result of asexual growth; (2) Very many of the antheridial sections, though possessing roots when planted, either died immediately or appeared to fade and remain faded for weeks, reviving only by sending out branches. The archegonial sections, on the contrary, though rootless when planted, as a rule quickly produced roots and grew rapidly.

Since there appears to be no way of dividing prothalli that offers any certainty that the organs cut away will not be regenerated, it is evident that in attempting to cross species of ferns that method of dividing and bringing prothalli together is best in which the prothalli offer most quickly facilities for cross-fertilization, in order that it may take place before regeneration of the organs. As antheridial sections that die or fade cannot be said to offer such facilities, in the experiments described further on whole prothalli have been substituted for the antheridial sections. In cutting the archegonial sections the incision has been made transversely close to the sinus of each prothallus in order to make certain of retaining archegonia only on the archegonial sections. Then, discarding the section containing antheridia, the archegonial section of a prothallus of one species has been planted against a whole pro-

FIG. 1. × 4. The letters in the series uniformly refer to the same plants: *A*, *Asplenium platyneuron*; *B*, hybrid artificially produced; *C*, *Asplenium ebenoides*; *D*, *Camptosorus rhizophyllus*.

thallus of the other species with the lower surfaces of the prothalli pressed close together, in the hope that when antherozoids should be set free on the whole prothallus some would reach and cross-

fertilize the archegonia on the archegonial section before that section could regenerate antheridia of its own.

It is obvious that in seeking to discover the origin of *A. ebenoides* the removal of organs of *A. platyneuron* or *C. rhizophyllus* is only of use in so far as it may facilitate cross-fertilization, for *A. ebenoides*, while it combines characteristics of these two ferns and hence might be produced by their cross-fertilization, is so distinct from either that it could not possibly be produced by the cross-fertilization of either. For the same reason it could not be produced by the asexual growth of either. Therefore if a plant of *A. ebenoides* should spring from prothalli of *A. platyneuron* and *C. rhizophyllus* that had been planted together and pure cultures had been insured, that plant must be considered proof that *A. ebenoides* is a hybrid between *A. platyneuron* and *C. rhizophyllus*.

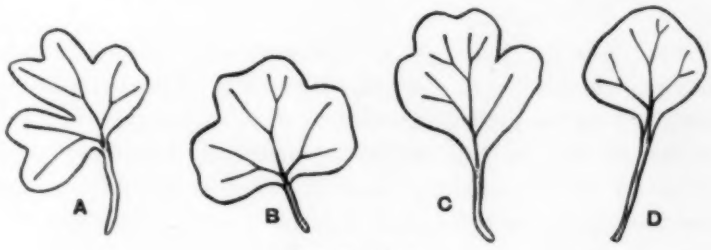

FIG. 2. × 4.

In order to insure pure cultures, in my experiments the prothalli have been raised on sterilized earth in new flower-pots and kept under glass. Lack of success during several years in crossing *A. platyneuron* and *C. rhizophyllus* has not been caused by prothalli of these ferns failing to produce a hybrid when planted together, but by the difficulty in getting prothalli of both ferns in proper condition at the same time in order to plant them together. Almost as soon as that was overcome results followed.

In the winter of 1900–1901 spores of these two ferns sown in separate flower-pots developed prothalli in large numbers. During February and March archegonial sections were cut from the prothalli of *C. rhizophyllus*, planted in a third pot, and a whole prothallus of *A. platyneuron* planted close against each section. In a fourth pot archegonial sections of *A. platyneuron* were planted

against whole prothalli of *C. rhizophyllus*. In a fifth pot a few whole prothalli of both ferns were planted against each other. In all about fifty pairs of prothalli were planted.

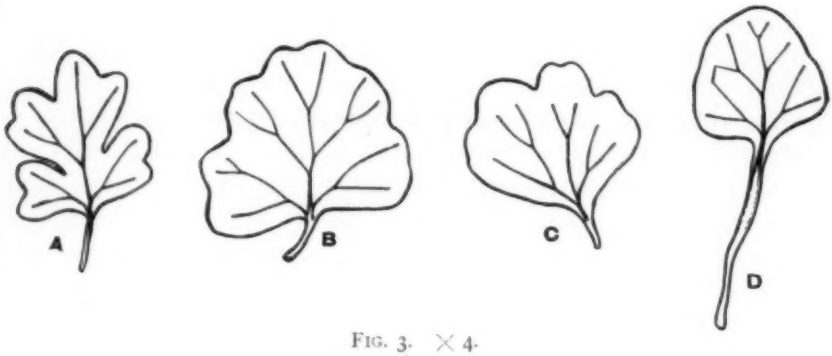

FIG. 3. × 4.

Now, if in the third pot antherozoids were set free on one of the whole prothalli of *A. platyneuron* and some were to fertilize the archegonia on the archegonial section of *C. rhizophyllus* in contact with that prothallus, in all probability some also would fertilize the archegonia on the whole prothallus. Hence, should a hybrid-plant develop, we would expect a plant of pure *A. platyneuron* to

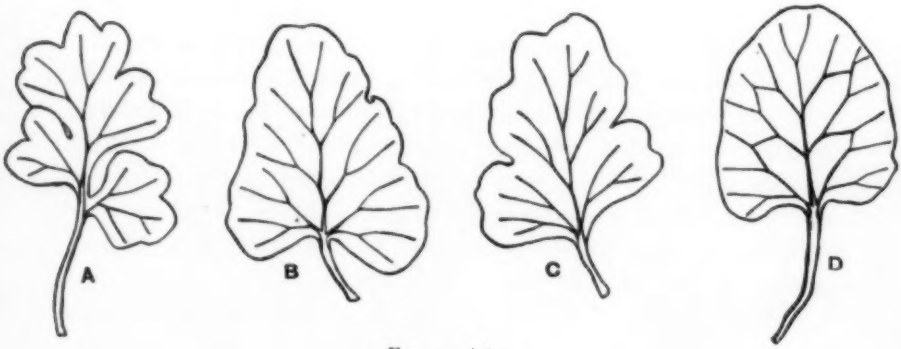

FIG. 4. × 4.

develop at the same time. That is what occurred. In June a plant, unquestionably a hybrid between *A. platyneuron* and *C. rhizophyllus*, and a plant of pure *A. platyneuron* sprang up side by

side.* It is probable, then, that this hybrid-plant was produced by archegonia of *C. rhizophyllus* fertilized by antherozoids of *A. platyneuron*. The following September a second hybrid-plant sprang up, but, as in the meanwhile plants both of pure *A. platyneuron* and of pure *C. rhizophyllus* had been produced, the organs cut away had probably been regenerated, hence no conclusions can be formed as to whether this second plant is the result of the same cross as the first or of the reciprocal cross.

FIG. 5. × 1½.

Shortly before September, from the appearance of plants of pure *C. rhizophyllus* and pure *A. platyneuron* in the fourth pot, it became evident that in that also the organs cut away had probably been regenerated, so for convenience the contents of the fifth pot were transferred to the fourth one. Two hybrid plants sprang up in it soon afterward, about the same time that the second hybrid plant appeared in the pot with the June plant.

The only fact that could lead one to suppose that the hybrid plants in the two pots might represent reciprocal crosses is that in the one containing the June plant the leaves of both plants, when young, were truncate at the base, like leaves of young *A. platy-*

* In this connection it is interesting to note that a pocket of rock containing a plant of *A. ebenoides*, found by G. A. Woolson in Vermont, contained also a plant of *A. platyneuron*.

neuron, and in the other cuneate, like leaves of young *C. rhizophyllus*. Later, the leaves of all four became cordate at the base, like leaves of mature *C. rhizophyllus*.

There can be no doubt of the hybridity of these four plants: they have shown from the beginning a most curious combination of the characteristics of *A. platyneuron* and *C. rhizophyllus*.

The leaves have varied from suberect to almost decumbent and, though none have taken root, some have rested their tips upon the earth.

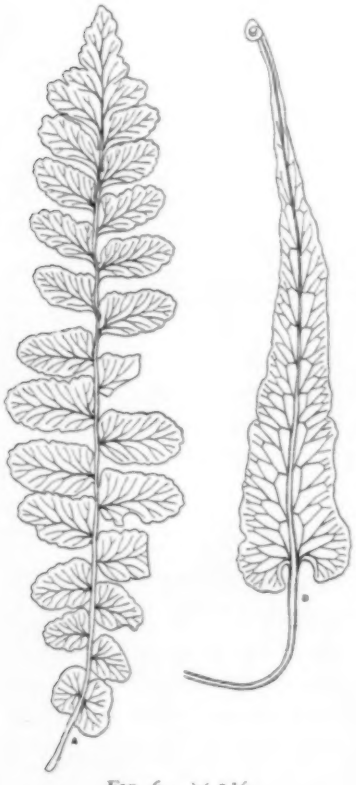

FIG. 6. × 1½.

That the leaf-blades are intermediate in outline between the leaf-blades of *A. platyneuron* and *C. rhizophyllus* may be seen from figures 1–7, in which the three ferns are shown in somewhat parallel stages of development, *A* representing leaves of *A. platyneuron*, *B* and *BB* in *f.* 1, 2, 3, 4 and 7 leaves of the June plant of the hybrid, *B* in *f.* 5 a leaf, of one of the September plants of the hybrid from the fourth flower-pot, and *D* leaves of *C. rhizophyllus*. The blades of the leaves of the hybrid combine fairly their texture, which is characteristic of *A. platyneuron* but not of *C. rhizophyllus*, with veins forming slightly raised lines on the face of the leaf, which is characteristic of *C. rhizophyllus* but not of *A. platyneuron*. Their color, though a lighter and brighter green than that of *C. rhizophyllus*, suggests it.

In one of the hybrid-plants in each pot the veins have been wholly free, and in the other, especially in the June plant, the veins, though mostly free, have formed a number of areolae.

In all three ferns when very young the petioles are green,

but other coloring soon appears at their bases and spreads upward. In *A. platyneuron* this coloring is at first light stramineous and spreads rapidly, involves in time the entire rachis and turns chestnut brown or purplish-ebeneous, sometimes leaving touches of green. In *C. rhizophyllus* it seems to vary from light to dark brown and extends, ultimately, only part way up the petiole. In the hybrid it has been brown from the beginning, has now a dark purplish tinge, and extends some distance up the back of the rachis. The petioles themselves in *C. rhizophyllus* are more or less narrowly winged on the sides, in the hybrid, they are similar, though perhaps more slender, while in *A. platyneuron* they are wingless.

The scales clothing the bases of the petioles in the three ferns are minute, acuminate, and reticulate in reddish-brown on an almost colorless background. In *C. rhizophyllus* they vary from lanceolate to lanceolate-deltoid or are occasionally ovate at base and narrowed suddenly above, and their margins are entire or sometimes bear short cilia. In *A. platyneuron* they are elongate-linear or lance-linear and their margins bear cilia often long and conspicuous. In the hybrid they are more or less intermediate in shape, resembling occasionally the scales of one parent more than those of the other, and their margins are entire or bear cilia varying in length.

On comparing the hybrid plants with a large number of specimens of *Asplenium ebenoides* from Havana Glen, Alabama, and from Virginia, and with photographs of *A. ebenoides* from Virginia, Maryland, and Vermont, I find that the characteristics of the hybrid are, with one exception, characteristics also of *A. ebenoides*. This exception is the manner in which the base of the blade of the leaf varies, at different stages of development, in its resemblance to that of *A. platyneuron* or of *C. rhizophyllus*. As already stated, in two of the plants of the hybrid when young the base of the blade resembled that of young *A. platyneuron* and in the other two that of young *C. rhizophyllus*, while in all four when older it resembled that of mature *C. rhizophyllus*. In young specimens of *A. ebenoides* from Havana Glen, the only young wild plant of this fern I have seen, the base of the blade resembles that of young *C. rhizophyllus*, while in older plants from Havana Glen

and elsewhere it resembles in some of the leaves that of mature *C. rhizophyllus* and in others that of mature *A. platyneuron*. But, supposing *A. ebenoides* and the hybrid to have arisen in the same way, for some of the progeny of the same parents to resemble one parent and for others at the same stage of development to resemble the other, is so common an occurrence that no comment is required. From the figures, in which *C* and *CC* represent leaves of *A. ebenoides* from Havana Glen, this varying resemblance of *A. ebenoides* and of the hybrid, at various stages of development, to *C. rhizophyllus* or *A. platyneuron* may be seen. It is especially noticeable in figures 1–3.

Of characteristics possessed by *A. ebenoides* and not by the hybrid I find but two:

1. Possession of sori. The lack of this characteristic in the hybrid is easily accounted for by the age of the plants. The plant are still growing and it is confidently expected that sori will develop upon older leaves.

2. Elongation and attenuation of the pinnae. But this characteristic is either not constant in *A. ebenoides* or else appears in different plants at different stages of development. It is very marked and seems to appear, as a rule, at an early age, in most specimens of *A. ebenoides* from Havana Glen. On the other hand, Dr. Murrill tells me that it did not appear in his plants from Virginia until they had been kept for some time in a greenhouse, in a favorable environment which caused them to develop luxuriantly. In one of his specimens that show no trace of it the blade of the leaf is fully 10.797 cm. long, about a third longer than that of the largest leaf of the hybrid plants, and well fruited. None of the leaves of the specimens of *A. ebenoides* found by Dr. C. E. Waters in Maryland show elongation and attenuation of the pinnae. So the utmost that can be said of the lack of this characteristic in the leaves of the hybrid is that they resemble some leaves of *A. ebenoides* rather than others. How close the resemblance is may be seen by comparing *B* and *BB*, *f.* 7, which represent leaves of the hybrid, with *C* and *CC*, *f.* 7, which represent leaves of *A. ebenoides*.

Thus, on comparing with *A. ebenoides* a fern produced by crossing *A. platyneuron* and *C. rhizophyllus*, it is found similar to

A. ebenoides in habit, coloring, texture, form of the leaf, venation, and character of the scales ; in short, it does not possess one characteristic that *A. ebenoides* does not possess at some time in its life history, and, though young, lacks of the characteristics of *A. ebenoides* only the possession of sori and elongation and attenuation of the pinnae, both of which are often absent in *A. ebenoides* at the same age. Surely we have here convincing proof of the origin of *A. ebenoides.*

FIG. 7. × 1½.

I am indebted to Dr. Lucien M. Underwood not only for the privilege of examining his collection of specimens of *A. ebenoides* from Havana Glen, but also for many courtesies extended to me in the preparation of this paper ; to Mr. William R. Maxon for a generous number of additional specimens of *A. ebenoides* from Havana Glen ; to Dr. W. A. Murrill for a photograph of *A. ebenoides* from Virginia and the loan of specimens and manuscript notes ; to Dr. H. H. Swift for photographs of *A. ebenoides* from Vermont, and to Dr. C. E. Waters for photographs of *A. ebenoides* from Maryland.

Hepaticae of Puerto Rico

I. THE SPECIES OF LEPTOLEJEUNEA, INCLUDING AN ACCOUNT OF THEIR VEGETATIVE REPRODUCTION

By Alexander W. Evans

(With Plates 23–25)

The genus *Leptolejeunea* is composed of minute tropical species which occur almost invariably on living leaves. A few of the species grow on ferns or on hairy plants, but most of them prefer the smooth and glossy evergreen leaves of trees and shrubs. They confine themselves to the upper surface of the leaves and at first form circumscribed patches, which are clearly defined. As the plants grow older the patches become confluent and lose their distinct outlines. The sterile axes of *Leptolejeunea* together with their leaves are at first very closely appressed to the matrix, but some of the later branches are ascending and those bearing perianths are suberect. The plants, however, never become densely matted together as is usual in the Lejeuneae.

The genus has several peculiarities in common with *Drepanolejeunea*. The underleaves for example are essentially the same in both and afford a convenient character for distinguishing them from other minute Lejeuneae. These underleaves are commonly minute even for the size of the plant and are built up in a very regular way. We can distinguish in them two slender divisions and a basal portion, the latter consisting of a central rhizoid-bearing region surrounded (except at the base) by a single row of marginal cells. The basal portion is usually in the form of a trapezium and is attached to the axis by the shorter of its parallel sides. In some species it is more nearly rectangular and is then abruptly contracted just above the base. From the upper angles of this basal portion arise the two filiform or subulate divisions, which are sometimes composed of a single row of cells throughout and are sometimes two or three cells wide in the lower part. The divisions vary from suberect to widely spreading and in certain species form an angle of 180° or more with each other. In the

latter case the upper boundary of the underleaf is a straight or slightly convex line. The number of cells in the basal portion, the number of cells in the divisions and the angle which the divisions form with each other vary within very narrow limits for a given species and are of much value in distinguishing between closely related plants. The rhizoids to which the underleaves give rise are numerous and of the usual type. They consist of simple or branched projections from the median cells of the basal portion and are not themselves divided into cells. The rhizoids secrete a gelatinous substance by means of which they attach the hepatic to its substratum. In a few species of *Drepanolejeunea* an underleaf sometimes develops a small, sucker-like disc, from which the rhizoids develop secondarily. Similar discs occur on the underleaves of *Odontolejeunea* * and also on the first underleaves of the leafy propagula in both *Leptolejeunea* and *Drepanolejeunea*.

In the position of the ♀ inflorescence and in the general characters of the perianth, *Leptolejeunea* also agrees with *Drepanolejeunea*. The ♀ inflorescence is borne on an extremely short branch, which in some species is simple and in others gives rise to a single innovation. With the exception of the perichaetial bracts and bracteoles the leaves on the ♀ branch are abnormally developed or rudimentary, and are commonly reduced to a single sideleaf and an underleaf. The perianth is dilated and sharply five-keeled in the upper part, and the keels, with rare exceptions, extend outward, and often slightly upward, as distinct projections or horns.

The most reliable differences between the two genera are to be found in the shape of the leaves and in the characters drawn from the keels and horns of the perianths. In *Leptolejeunea* the leaves are gradually dilated from a narrow base and are rhombic, ovate, or lanceolate in outline; their apices, although sometimes acute, are scarcely acuminate and are usually plane. In *Drepanolejeunea* the leaves are abruptly dilated from a still narrower base, and are more or less triangular in outline, their apices are long and slender and usually reflexed. In *Leptolejeunea* the keels and horns of the perianth are smooth or nearly so, while in *Drepanolejeunea*, they

* *Cf.* Spruce, Hep. Amaz. et And. 142. 1884. Also Goebel, Pflanzenbiologische Schilderungen, 1: 161. *f.* 66. 1889.

are rough and often spinose. In *Leptolejeunea* also the leaves are usually ocellate and the inflorescence autoicous, while in *Drepanolejeunea*, the leaves are rarely ocellate and the inflorescence is usually dioicous. It must be admitted, however, that there are species which it is difficult to assign definitely to either genus, and in such cases we must rely upon a combination of characters rather than upon any single generic difference.

Four species of *Leptolejeunea* are now known from Puerto Rico, all of which are widely distributed in the American tropics. The commonest of these is probably *L. elliptica*, which has already been recorded by Stephani. * The range of this abundant species extends through the islands of the Pacific into the East Indian archipelago.

Leptolejeunea exocellata (Spruce)

Lejeunea (*Lepto-Lejeunea*) *exocellata* Spruce, Hep. Amaz. et And. 195. 1884.

Pale green, becoming brownish upon drying; stems 0.05 mm. in diameter, closely adherent to substratum, once to thrice pinnate with widely spreading branches but less copiously branched than the preceding species: leaves distant, the lobe widely spreading, plane or nearly so when moist, appressed to substratum, ovate to obovate, 0.45 mm. long, 0.25 mm. wide, attached by a very short, oblique line of insertion, margin entire or nearly so, antical margin not arching across axis, apex obtuse to subacute; lobule oblong-rhomboidal, inflated, 0.14 mm. long, 0.09 mm. wide, keel slightly arched or almost straight, usually continuous with postical margin of lobe, roughened from projecting cells, free margin plane, appressed to basal ocellus of lobe, bicrenulate at the apex, then passing by a straight line or by a lunulate sinus to end of keel: leaf-cells thin-walled, plane or nearly so, averaging 15 μ in diameter at edge of lobe and 19 μ in the middle and at the base, trigones and intermediate thickenings minute but usually distinct, never confluent; basal ocellus, the only one present, 50 μ long, 27 μ wide, projecting postically and forming a cylindrical water-sac with the plane lobule, usually overlapped and almost covered over by adjacent cells of lobe: underleaves distant with erect or

* Hedwigia, 27: 285. 1888.

obliquely spreading, filiform divisions, each consisting of 3 or 4 cells in a single row, basal portion of underleaf rectangular or tapezoidal, 0.05 mm. long, 0.07 mm. wide, abruptly narrowed at the base, radicelliferous region surrounded by 6 marginal cells, 3 on each side, basal marginal cells curved inward, second marginal cells forming the rounded lower angles of the basal portion, third marginal cells meeting in the middle and giving rise at their junction with the second cells to the filiform divisions of the underleaf: inflorescence autoicous: ♀ inflorescence borne on a very short branch without innovation; leaf at base of branch smaller than ordinary leaves, the lobe ovate to rotund, the lobule reduced to a single row of cells connate with the lobe; underleaf at base of branch broadening from a narrow base, bifid about one half with subulate lobes and a broad lunulate sinus; bracts suberect or obliquely spreading, scarcely complicate, unequally bifid with narrow, long-pointed lobes and lobules, the lobes 0.45 mm. long, 0.07 mm. wide, margin entire; bracteole connate on both sides at the base, linear, shortly bifid with subacute divisions and sinus, margin entire, 0.35 mm. long, 0.07 mm. wide above connate base; perianth somewhat exserted, oblong or obconical from a narrow base, broad at the apex and with a short beak, 0.5 mm. long, 0.45 mm. wide in upper part, terete below, sharply five-keeled above, the keels extending upward and outward as acute or truncate horns, smooth or slightly roughened near the apex: or inflorescence usually occupying a short branch, rarely terminal on a leading branch; bracts usually in 2 or 3 pairs, imbricated, strongly inflated, shortly and subequally bilobed with obtuse divisions, keel crenulate or denticulate from projecting cells; bracteoles present at base of spike, bifid about one half with subulate lobes and obtuse or subacute sinus; antheridia in pairs: mature sporophyte not seen (*pl. 23*).

On living leaves. Between Cayey and Aibonito, *Heller* (568, 569); near Mayaguez, *Heller* (4566 *p. p.*, 4567 *p. p.*); Cayey, *Evans* (70a *p. p.*).

LEPTOLEJEUNEA ELLIPTICA (Lehm. & Lindenb.) Schiffn.

Jungermannia elliptica Lehm. & Lindenb.; Lehmann, Pugillus, **5**: 13. 1833.

Lejeunea elliptica Lehm. & Lindenb.; G. L. & N. Syn. Hep. 403. 1845.

Colura elliptica Trevis, Mem. r. Ist. Lomb. III. **4**: 402. 1877.

Lejeunea (*Lepto-Lejeunea*) *elliptica* Spruce, Hep. Amaz. et And. 194. 1884.

Lepto-lejeunea elliptica Schiffn. Die nat. Pflanzenfam. **11**[3]: 26. 1893.

Pale green, becoming brownish or blackish upon drying; stems 0.04 mm. in diameter, closely adherent to substratum, once to thrice pinnate with widely spreading branches: leaves distant, the lobe widely spreading, plane or nearly so when moist, appressed to substratum, oblong-ovate to oblong-lanceolate, 0.35 mm. long, 0.18 mm. wide, attached by a very short oblique line of insertion, margin entire, antical margin not arching across axis, apex rounded, obtuse or rarely subacute; lobule ovate, inflated, 0.01 mm. long, 0.08 mm. wide, keel slightly arched or almost straight, usually continuous with postical margin of lobe, roughened from projecting cells, free margin plane and appressed to basal ocellus of lobe, bicrenulate at apex, then passing by a lunulate sinus to end of keel; lobule often poorly developed; leaf-cells thin-walled, plane or nearly so, averaging 13 μ in diameter at edge of lobe and 23 μ in the middle and at the base, trigones and intermediate thickenings minute but distinct, never confluent; ocelli 2 to 5 in number, arranged in a median, interrupted line, basal ocellus larger than the others, 45 μ long, 25 μ wide, projecting postically and forming a cylindrical water-sac with the plane lobule, sometimes partially overlapped by adjacent cells of lobe: underleaves distant with widely spreading, filiform divisions, each consisting of 2 or 3 cells in a single row, the cells longer than in *L. exocellata* and with less bulging walls, basal portion broadly rectangular or trapezoidal, 0.04 mm. long, 0.07 mm. wide, abruptly narrowed at the base, radicelliferous region surrounded by 6 marginal cells as in the preceding species but with the second marginal cells sharply angular instead of rounded: inflorescence autoicous or dioicous: ♀ inflorescence borne on a very short branch without innovation; leaf and underleaf at base of branch similar to those of *L. exocellata*; bracts obliquely spreading, scarcely complicate, shortly and unequally bifid, the lobe oblong to obovate, acute to rounded at the

apex, sometimes indistinctly apiculate, entire, 0.4–0.5 mm. long, 0.08–0.14 mm. wide, lobule ovate to ligulate, obtuse; bracteole connate on both sides at the base, linear, shortly bifid with obtuse sinus and obtuse or acute divisions, margin entire, 0.25 mm. long, 0.07 mm. wide above connate base; perianth slightly exserted, obconical from a narrow base, broad at the apex and with a short beak, 0.4 mm. long, 0.35 mm. wide, terete below, sharply fine-keeled above, the keels extending upward and outward as acute or truncate horns, smooth or slightly roughened near the apex; or inflorescence usually occupying a short branch, rarely terminal on a leading branch; bracts and bracteoles as in *L. exocellata;* antheridia in pairs: spores oblong, greenish, with a thick, brownish, minutely verruculose wall, averaging 23 μ in short diameter (*pl. 24, f. 1–7*).

On living leaves. First collected by *Sintenis* (45, 136); 14 miles south of San Juan, *Heller* (678, 680); near Mayaguez, *Heller* (4566 *p. p.*, 4567 *p. p.*); Cayey, *Evans* (70a *p. p.*).

L. exocellata and *L. elliptica* are very closely related species. They are not only strikingly similar in appearance but are likely to grow mixed together on a single leaf, and for these reasons they have been much confused by students of the hepaticae. Even Spruce, who first recognized the first species, considered its validity as somewhat doubtful and suggested that it might perhaps be looked upon as a variety of *L. elliptica.*

According to its author, *L. exocellata* may be distinguished from *L. elliptica* by the following differences: the plants are a little larger, their leaves are sometimes narrowed at the base (*i. e.*, obovate-lanceolate) and are constantly *exocellate*, the leaf-cells are more indistinct and with somewhat thickened walls, the infrafloral underleaf is conspicuously pentagonal and bicuspidate, the perichaetial bracts are narrower and the perianth is larger.

Unfortunately several of these differences are not to be relied upon, and this applies particularly to those which concern the leaf-cells. In his full descriptions of the two species in question, Spruce states that the cells of *L. elliptica* are "valde leptodermes," while those of *L. exocellata* are "intus sinuatae, parietibus, subincrassatis." As a matter of fact the cell-walls are very thin in both species but show almost invariably minute and distant trigones

and intermediate thickenings. These are a trifle larger in *L. elliptica* than in *L. exocellata*, but the difference is not at all striking. The species of *Leptolejeunea* when dried do not always assume their natural appearance upon the addition of water. Even boiling water is not always effective, and it is sometimes necessary to treat them with potash solution or some similar reagent before we can gain an accurate idea of their cells. This is probably one reason why the cell-structure is not always accurately described.

The absence of ocelli in the leaves of *L. exocellata* is emphasized by Spruce, and it is from this supposed character that the species derives its name. There is present, however, at the base of the lobe a large hyaline cell about three times as long as the neighboring cells. This cell, which would naturally be interpreted as an ocellus, occurs not only in Puerto Rico specimens, but also in South American specimens distributed by Spruce himself. The ocellus is more or less overlapped by the adjacent part of the lobe on the side toward the keel. This part is distinctly convex, and we can see the ocellus clearly only by focussing through the cells which lie over it (*pl., f. 4*). Sometimes the overlapping goes so far that the ocellus looks as if it were a foreign body inside the water-sac, and possibly it has been so interpreted. In reality it takes direct part in the formation of the water-sac. It is not only longer than the neighboring cells, but greater in diameter and projects considerably beyond them toward the substratum. Here it comes into contact with the free edge of the lobule, which remains plane or nearly so (*f. 5*), and in this way a cylindrical sac is formed open only at one end. The capacity of the sac is of course increased by the convexity of the lobe between the ocellus and the keel. A similar ocellus occurs in *L. elliptica*, but it is usually less concealed by overlapping cells. Except for this basal ocellus the leaf of *L. exocellata* is truly "exocellate," and lacks the interrupted row of ocelli, which is characteristic of *L. elliptica*.

The differences in the subfloral underleaves, as noted above, do not seem to be constant. It is sometimes difficult to make out these structures at all on account of the numerous rhizoids which they bear, but when well developed they are essentially alike in the two species.

The remaining differences mentioned by Spruce seem to be

trustworthy. It may be added to these that the leaves of *L. elliptica* are usually from 8 to 12 cells broad, while those of *L. exocellata* are from 12 to 15 cells. The underleaves of the latter species also are rounded below instead of angular, and their slender divisions spread less widely and have more bulging cells than in *L. elliptica*.

LEPTOLEJEUNEA STENOPHYLLA (Lindenb. & Gottsche) Schiffn.

Lejeunea stenophylla Lindenb. & Gottsche; G. L. & N. Syn. Hep. 769. 1847.

Colura stenophylla Trevis, Mem. r. Ist. Lomb. III. **4**: 402. 1877.

Lejeunea (*Lepto-Lejeunea*) *stenophylla* Steph. Hedwigia, **29**: 96. 1890.

Leptolejeunea stenophylla Schiffn. Engler's Bot. Jahrb. **23**: 596. 1897.

Pale green, becoming yellowish or brownish upon drying; stems 0.035 mm. in diameter, closely adherent to substratum, irregularly once or twice pinnate with widely spreading branches: leaves distant, the lobe obliquely spreading, plane or somewhat revolute along antical margin, straight or upwardly curved near the apex, lanceolate, 0.5 mm. long, 0.13 mm. wide, somewhat narrowed toward the base and attached by an almost longitudinal line of insertion, margin entire or very slightly crenulate or denticulate from projecting cells, apex acute or short acuminate; lobule ovate, strongly inflated, 0.12 mm. long, 0.09 mm. wide, keel slightly arched, smooth or nearly so, usually continuous with postical margin of lobe, free margin plane or strongly involute too, or including the apex, then lunulate to end of keel, apex formed by a single cell so strongly curved as to almost touch the end of the keel, forming in this way a circular opening into the water-sac; lobule often poorly developed; leaf-cells thin-walled and without trigones, plane or nearly so, averaging 17 x 12 μ at the edge of lobe and 20 x 12 μ in the middle and at the base; ocelli 1 to 4, forming an interrupted median row, scarcely distinguishable from the other cells: underleaves distant, 0.04 mm. long, 0.15 mm. wide, with widely spreading filiform divisions, each consisting of (2 or) 3 cells in a single row, basal portion of underleaf broadly trapezoidal, cuneate at the base, the lateral margins continuous with the divisions, radicelliferous region surrounded by 6 marginal cells: inflorescence dioicous: ♀ inflorescence borne on a very short branch, innovating on one side with

a short, simple and sterile innovation; bracts obliquely spreading, scarcely complicate, unequally bifid, the lobe ovate, acute or acuminate, 0.35 mm. long, 0.12 mm. wide, margin irregularly denticulate, lobule varying from sharp-pointed to truncate, 0.17 mm. long, 0.009 mm. wide, margin as in lobe; bracteole more or less connate on both sides at the base, narrowly ovate, 0.35 mm. long, 0.1 mm. wide, bifid about one third with narrow, erect sharp-pointed lobes, and a narrow sinus, margin denticulate; perianth somewhat exserted, obconical, gradually narrowed toward base, 0.6 mm. long, 0.35 mm. wide, broad and truncate at the apex, and very shortly beaked, terete below, sharply 5-keeled above, the keels extending outward as triangular horns, acute to truncate at the apex, smooth or slightly roughened from projecting cells: or inflorescence occupying a short branch or terminal on a leading branch; bracts usually in 6 to 10 pairs, imbricated, strongly inflated, shortly and subequally bifid, the lobe obtusely to acutely pointed, lobule blunter, keel strongly arched, cells in upper part forming a very narrow denticulate wing: bracteoles present at base of spike, small, bifid about one half, with erect-spreading pointed lobes and obtuse sinus: antheridia in pairs: mature sporophyte not seen (*pl. 24, f. 8–16*).

On living leaves. Cayey, *Evans* (70b).

The specimens of *L. stenophylla* from Puerto Rico agree very closely with those distributed in Hepaticae Cubenses Wrightianae. The latter were determined by Gottsche and the determination has since been confirmed by Schiffner. The species has also been reported from Mexico (the type-locality) and from Bolivia.

L. stenophylla is very distinct from the two preceding species. It differs from them in its leaves, which are narrower and much more sharply pointed; in its leaf-cells, which lack local thickenings; in the absence of a large basal ocellus; and in the presence of a subfloral innovation. Its underleaves also are very different in shape and are never angular below their spreading divisions. In its lobule, the apex of which is formed by a single strongly curved cell, the species differs not only from *L. elliptica* and *L. exocellata* but from nearly all the other members of the genus, and approaches in this respect several species of *Drepanolejeunea*.

LEPTOLEJEUNEA HAMULATA (Gottsche) Schiffn.

Lejeunea hamulata Gottsche; Wright, Hep. Cubenses; Schiffn. Engler's Bot. Jahrb. **23**: 587. 1897 (as synonym).

Leptolejeunea hamulata Schiffn. *l. c.*

Brownish-green, growing in thin, irregular patches: stems prostrate, 0.06 mm. in diameter, irregularly pinnate, the branches widely spreading, those bearing propagula microphyllous: leaves distant to contiguous, the lobe obliquely spreading, plane or with slightly revolute margins near the apex, ovate to ovate-lanceolate, distinctly narrowed toward the base, 0.6 mm. long, 0.25 mm. wide, attached by an almost longitudinal line of insertion, margin denticulate except in basal region, the teeth usually projections of single cells, rarely composed of from 1 to 3 cells, antical margin somewhat more convex than postical, apex acute, tipped with a single cell or with 2 superimposed cells; lobule oblong, 0.2 mm. long, 0.14 mm. wide, inflated toward base and along keel, plane and appressed to lobe in outer part, keel slightly arched, forming an almost continuous line with postical margin of lobe, free margin involute toward base, passing beyond apex by a lunulate sinus to end of keel, apex formed by a single, strongly curved cell separated by a slight indentation from the inner part of the free margin; cells of lobe plane or nearly so, averaging 14 μ at the edge, 23 x 13 μ in the middle and at the base, thin-walled throughout or more rarely with indistinct and more or less confluent local thickenings; ocelli indistinct, but present in well-developed leaves, varying in number from 1 to 6, usually 4, arranged in an interrupted longitudinal row, those near the base of lobe measuring 35 x 23 μ, those in outer part averaging 23 x 16 μ: underleaves distant, basal portion trapezoidal in outline, often abruptly contracted at base, 0.05 mm. long, 0.09 mm. wide, marginal cells 6, the second cells more or less bulging, divisions obliquely spreading, 3 or 4 cells long, 1 or 2 cells wide at base, the cells very slightly bulging, cluster of rhizoids sometimes replaced by a sucker-like disc: inflorescence dioicous: ♀ inflorescence borne on a very short branch, innovating on one side with a short, simple and sterile innovation; underleaf at base of branch usually with a sucker-like disc; bracts erect-spreading, complicate, shortly and unequally bifid, the lobe ovate, 0.45 mm. long, 0.2 mm. wide, acute, sharply and irregularly denticulate above the middle: lobule oblong, 0.35 mm. long, 0.1 mm. wide, truncate to acute at the apex, denticulate; bracteole connate on one side, oblong-obovate, 0.4 mm. long, 0.17 mm. wide, bifid about one third with acute divisions and sinus, margin irregularly denticulate or crenulate in upper part; perianth obpyramidal, shortly rostellate, 0.55 mm. long, 0.45 mm. wide at apex, 5-keeled, the keels dilated and truncate in upper part, smooth or nearly so: ♂ inflorescence terminal on a short branch; bracts in 5 to 12 pairs, imbricated, strongly inflated, shortly bifid, the lobe obtuse, the lobule rounded, margins subentire, keel strongly arched, denticulate in

outer part; bracteoles limited to base of spike, similar to ordinary underleaves, but smaller and with more erect divisions: antheridia in pairs (*pl. 25*).

On living leaves. Cayey, *Evans* (71 *p. p.*).

The Puerto Rico specimens of *L. hamulata* agree closely with those distributed in Hepaticae Cubenses. Unfortunately they show no perianths and the description of this organ as given above is taken entirely from Schiffner. In all other respects the specimens are well developed.

The close relationship which exists between the present species and *L. stenophylla* has already been commented upon by Schiffner. *L. hamulata* is the larger of the two species and differs also in its broader and less acuminate lobes with sharply denticulate margins. It must be acknowledged, however, that poorly developed specimens are sometimes difficult to determine.

In the original description of *L. hamulata* the lobule is said to be "cylindrico-convolutus apice duobus dentibus validis hamatis conniventibus foramen rotundum includentibus armatus." One of the teeth referred to is evidently the curved cell at the apex of the lobule, the other is apparently the fold at the junction of lobule and lobe. Until the lobule is flattened out by pressure this fold often resembles a tooth in a marked degree. A lobule of this character, although not unusual in *Drepanolejeunea*, is, according to Schiffner, almost unique in *Leptolejeunea*. He emphasizes it in fact as one of the most important differences between *L. hamulata* and *L. stenophylla*. It is evident, however, from a study of the Puerto Rico specimens of the latter species that a *normal* lobule is built up on essentially the same plan as in *L. hamulata*. Unfortunately normal lobules are somewhat unusual and are largely replaced by rudimentary structures in which the true lobular characters are not apparent. In the Cuban specimens normal lobules are still more infrequent but may be demonstrated by careful search.

Aside from their lobules *L. stenophylla* and *L. hamulata* resemble each other closely in their antheridial spikes, in the possession of a subfloral innovation, in their perichaetial bracts and bracteoles and apparently also in their perianths. Most of these peculiarities will distinguish them from *L. exocellata* and *L. elliptica*.

In addition to the ordinary method of reproduction, the four

Puerto Rico Leptolejeuneae exhibit a vegetative reproduction by means of leafy propagula. These arise just behind the leaves in the position usually occupied by normal branches. They are to be looked upon, therefore, as modified branches, the whole of the branch, with the exception of the basal sheath, taking part in the formation of the propagulum. Leafy propagula have already been noted in *Plagiochila* and in various other genera of the Jungermanniceae, but in all cases which have been described they have arisen directly from leaf-cells or more rarely from indefinitely situated axis-cells. Goebel * ascribes the formation of these propagula to the latent power retained by every cell of the liverwort (*i. e.*, of the gametophyte) to develop as if it were a spore—a power which is not made manifest until the plant becomes enfeebled. Propagula of this character are essentially different from those of *Leptolejeunea*, in which the reproductive bodies represent entire branches. The latter, although described for various mosses,† have not before been recorded for any of the leafy hepatics.

The modifications in structure which are exhibited by the propagula of *Leptolejeunea* are in part explicable by their function as reproductive bodies and in part by the peculiar habitat of the species, namely the smooth and glossy surface of evergreen leaves. These modifications are most pronounced in *L. exocellata* and *L. elliptica*, and the propagula of these two species, which are essentially alike, will be considered first. Instead of spreading widely as it would if it were a normal branch, a young propagulum grows toward the apex of the stem, lying above the leaves and parallel with the axis or only slightly diverging from it (*pl. 23, f. 9*). In assuming this position its axis curves abruptly near the base in such a way that the antical surface of the propagulum is turned downward, while the postical surface with its underleaves is turned upward.

The first few leaves and underleaves of the propagulum (*f. 10*) are very different from those borne on ordinary axes. The leaves, although larger than the first leaves of a normal branch, are shorter than typical leaves and are nearly as broad as long. Their

* Organographie der Pflanzen, 277. 1898.

† Cf. Correns. Unters. über die Vermehrung der Laubmoose durch Brutorgane und Stecklinge. 1899. *E. g.*, *Plagiothecium elegans*, p. 250.

lobes are strongly squarrose and are sometimes completely reflexed, so that they come to lie parallel with the axis and with their apices pointing toward the base of the propagulum. The lobules are very rudimentary and in the reflexed leaves are turned forward, in this way obliterating the keel. The modified leaves, instead of being entire like ordinary leaves, are angular-dentate with from one to three teeth, one being at the apex, and the others (when present) on the outer edge. These teeth often end in the curious rhizoid-like processes (*f. 11*) described by Schiffner * for *Cheilolejeunea versifolia* and for certain other hepaticae, but it is doubtful if they ever assume the function of rhizoids. As we pass from the base toward the apex of the propagulum, we find all gradations between these modified leaves and the ordinary leaves of the species.

The first two underleaves of the propagulum are perhaps even more remarkable than the leaves. They are larger than ordinary underleaves and their divisions often bend inward instead of diverging. The middle cells of the basal portion, which are more numerous than usual, do not produce rhizoids directly but develop instead, a large, orbicular, sucker-like disc (*f. 12*) composed of minute and closely united cells. This disc is entire on the margin and often projects slightly beyond the basal portion of the underleaf.

When a propagulum has developed several pairs of leaves, it becomes separated from the parent plant and develops into a new individual. The separation takes place at its junction with the parent-axis just within the basal sheath. The cells by which it is actually attached are few in number, often reduced apparently to a single one. These cells gradually become shriveled, and it requires very little force to tear them across and set the propagulum free. Probably in nature the force of a shower would be sufficient to bring about this result. It has already been stated that a propagulum, while still attached, lies withits underleaves turned away from the substratum. This position cannot be very stable after separation takes place, because the propagulum would rest on nothing except the edges and apices of its squarrose leaves. Probably here again the force of dripping water is sufficient to over-

* Engler's Bot. Jahrb. 23 : 598. *pl. 15. f. 4.* 1897.

turn it and at the same time to carry it a short distance away from its parent axis.

By means of the discs on the underleaves, which have the power in common with rhizoids of secreting a gelatinous substance, the propagulum attaches itself firmly to the substratum. Sometimes the attachment is made still firmer by rhizoids which grow out from the marginal cells of the disc (*f. 13*). In the similar discs of *Odontolejeunea* the power of developing rhizoids is possessed by all the cells of the disc, instead of by the marginal cells alone, as in these propagula. When the propagulum has thus established itself, its growing region continues to develop and produces an axis bearing normal leaves and underleaves.

The propagula of *L. stenophylla* are less highly specialized than those of the two preceding species. The branches upon which they are developed usually bear abortive leaves, consisting of a short lobe and an extremely rudimentary lobule, and the growth of these branches is soon arrested by the production of the propagula. In this species the first underleaf is larger than the succeeding ones and shows a well-developed disc. The lobes of the first and second side-leaves are squarrose and more or less toothed and the lobule of the first leaf at least is very rudimentary. The third leaf, however, and sometimes even the second, develop normal lobules, and the fourth and fifth leaves show fairly characteristic lobes.

Leafy propagula of the type just described occur also in several species of *Drepanolejeunea*. Their discovery may likewise be expected in other epiphyllous Lejeuneae and especially in those which do not develop disc-shaped gemmae.

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Explanation of Plates

The figures were drawn by the writer with the aid of the camera lucida. Most of them were prepared for reproduction by Miss Edna L. Hyatt.

PLATE 23

Leptolejeunea exocellata (Spruce) Evans. 1. Stem with two perianths, a ♀ inflorescence and a ♂ inflorescence, postical view, × 47. 2. Cells from middle of lobe, × 425. 3. Cells from apex of lobe, × 300. 4. Cells from base of lobe, showing basal ocellus partially overlapped by adjacent cells, × 400. 5. Transverse section through lobe and lobule, showing basal ocellus, × 300. 6. Apex of lobule, × 300.

7. Underleaf, × 300. 8. Bracts and connate bracteole, × 67. 9. Stems with three young propagula in various stages of development, × 47. 10. Base of an established propagulum, × 47. 11. Apex of one of the first leaves of a propagulum, × 300. 12. Underleaf of propagulum with sucker-like disc, × 360. 13. Marginal cells of disc with rhizoids, × 360. Ten was drawn from a specimen collected by A. A. Heller near Mayaguez (no. 4567 *p. p.*); the other figures were all drawn from specimens collected by the writer at Cayey (no. 70a *p. p.*).

PLATE 24

Leptolejeunea elliptica (Lehm. & Lindenb.) Schiffn. 1. Part of plant with perianth, postical view, × 45. 2. Cells from middle of lobe, enclosing an ocellus, × 400. 3. Cells from base of lobe showing basal ocellus, × 280. 4. Apex of lobule, × 280. 5. Underleaf, × 280. 6. ♀ branch, postical view, × 65. 7. Bracts and connate bracteole, × 65. The figures were all drawn from specimens collected by A. A. Heller near Mayaguez (no. 4567 *p.p.*).

Leptolejeunea stenophylla (Lindenb. & Gottsche) Schiffn. 8. Stem with perianth, postical view, × 45. 9. ♂ inflorescence, postical view, × 45. 10. Cells from middle of lobe, enclosing an ocellus, × 400. 11. Cells from apex of lobe, × 280. 12. Cells from antical margin of lobe, × 280. 13. Apex of lobule, × 280. 14. Underleaf, × 280. 15. Bract and connate bracteole, × 65. 16. Perianth, × 45. The figures were all drawn from specimens collected by the writer at Cayey (no. 70b).

PLATE 25

Leptolejeunea hamulata (Gottsche) Schiffn. 1. Stem with ♀ inflorescence, postical view. 2. Part of stem, antical view. 3. Cells from middle of lobe. 4. Cells from antical margin of lobe. 5. Cells from apex of lobe. 6. Outer portion of lobule. 7. Underleaf. 8. Bract and bracteole. 9. Bract from same involucre. 10. Microphyllous branch showing a propagulum almost ready to become separated and the empty sheath of several older propagula, postical view. 11. An established propagulum, becoming microphyllous in upper part. All the figures are drawn from specimens collected by the writer at Cayey.

The saltatory Origin of Species

By Charles A. White

The following remarks refer to certain noteworthy cases of sudden specific mutation in the genus *Lycopersicum*, and the correlated production of a new horticultural variety of tomato. These remarks will be followed by a comparison of the phenomena referred to with the mutation theory of Professor de Vries and with some of the results of his demonstrative experiments.*

Without reference to the eight or nine other species of tomato that have been more or less satisfactorily recognized by botanists, *Lycopersicum esculentum* has, under American cultivation, become divided not only into a very large number of horticultural varieties, but into at least three distinct groups of those varieties. The varieties, as recognized by gardeners, are mainly, but not wholly, characterized by differences in quality, size and color of the fruit; but the groups are phylogenetic in character and readily recognizable by differences of foliation and inflorescence, and of general habit and relative size of the plants. The color consistence form and size of the fruit, being varietal characters only, are not the exclusive property of any one of these three groups. Two of the groups are known to have originated from the other one; and each one of them embraces a part of the many known varieties. The groups are so distinct from one another, and are characterized by such definite and heritable attributes, that if they had been found in the wild state, no botanist would hesitate to give them new specific names. Their origination under cultivation does not justify one in refusing to apply such names because horticulture does not change the mutative nature of plants. Its nurture and protection give more freedom for normal mutation, as well as for fluctuating and racial variation, than could occur in the wild state. Still, for descriptive purposes in the first part of this article, I will give them the non-systematic name of group,

* See Volume I. of Die Mutationstheorie. Versuche und Beobachtungen ueber die Entstehung von Arten im Pflanzenreich. Von Hugo de Vries. Leipzig, 1901.

and designate them as the atavic, solanoid and latifoliate groups respectively.

The atavic group embraces those decumbent, more or less diffuse, plants with loose foliage, which represent *Lycopersicum esculentum* as it was first horticulturally known, and which now includes the majority of the most approved fruit-varieties. The solanoid group embraces those plants which are often sturdy and more or less upright in posture, and whose compact, rugose foliage has come to be known as the "potato-leaf." It is because the general aspect of the plants often suggests *Solanum* rather than *Lycopersicum* that this group name is given. The solanoid group embraces a considerable number of varieties, but not so many as does the atavic group. A conspicuous feature of the latifoliate group is the character of its leaves, whose petioles are decurrent and whose leaflets are few in number, broad, flattened, and sometimes have their borders entire. The most characteristic member of this group is the variety known to gardeners as the Mikado. It is also sometimes called Turner's Hybrid, but because it is so conspicuously unlike either of its parent forms I think it really originated in correlation with the specific mutation which produced the latifoliate group, and not by hybridization. Other known members of this group are yet very few. The members of each of these three groups are more or less true to their own seed as regards the characteristics of both group and variety, but the cases of sudden mutation which I am about to describe constitute a special deviation from that rule as do also the cases of original mutation, which produced in correlation with that act, the first varieties of the solanoid and latifoliate groups.

My observations were made while engaged in amateur gardening upon my house-lot in Washington, D. C., and were briefly as follows: In the spring of 1898 I purchased from a dealer in Washington two dozen tomato plants of the Acme variety and transplanted them in my small garden. They produced a uniform crop, both fruit and plants answering in all respects to the reputed characteristics of the Acme, the plants of which variety are typical representatives of the atavic group. I selected seeds from fruit of the best plants of the crop and planted them in the same garden plot in 1899, expecting to grow another crop of Acme tomatoes

from them. The seeds germinated promptly and the crop of thirty young plants grew well, but from their first appearance above ground they showed a marked difference from Acme plants. When they had reached the fruiting stage they had developed into typical representatives of the solanoid group, and not of their parent atavic group ; showing that the difference from their parent form was more than varietal in character. Furthermore, every plant of that crop possessed identically the same characteristics, all having shared equally and fully in the mutation. The new form was varietally characterized by an excellent quality of fruit, but it was different in flavor and shade of color from that of the Acme, and ripened earlier than did that of the parent plants. I saved no seed from the fruit of the new variety and therefore supposed it to be lost, as indeed it was.

In 1900 I planted in the same garden-plot Acme tomato seed which I purchased from a seedsman who grew it on a Pennsylvania farm, more than a hundred miles from the place where the seed of my first crop was grown. These seeds also produced a uniform crop of typical Acme plants and fruit. I selected seeds from fruit of the best of that crop of thirty Acme plants and sowed them in my garden in the spring of 1901, and grew in that year also thirty plants from those seeds, again expecting to get a harvest of Acme tomatoes. On the contrary, the result was an exact duplication of my experience of 1899, every plant and every fruit partaking fully and uniformly in the duplicated mutation. *

One naturally inquires whether mutation of any other variety than the Acme would have occurred in my garden, whether it is an inherent quality of that variety to give only one mutative result, and that toward the Solanoid group, and what are the natural and artificial conditions of my garden. I have made no experiments with any other varieties than the Acme and its progeny, the new one, and can therefore only refer to these. The Acme variety is now about twenty-five years old, and has been one of

* An account of these two mutations of identical character was published in Science for November 29, 1901, but a sufficiently clear distinction between the combined varietal and specific characteristics of the plants resulting from that mutation was not therein made. That statement also was written from a horticultural rather than from a botanical standpoint.

the most stable of the many known varieties of tomato; but of late years it has shown so much tendency to atavic reversion that gardeners are abandoning its cultivation. Possibly that senile decline of varietal characters with which the true specific attributes were long blended, has left the latter with more freedom for mutation. Still, it cannot be supposed that such a condition is the rule for all mutating plants, and it will presently be shown that mutation sometimes occurs in the first generation of a species following its own origin by mutation.

Two dozen plants of the new variety from seed of the second mutation observed by me are now, July 15, 1902, growing vigorously in my garden and bearing characteristic fruit. Every plant is true to seed in both varietal and specific characteristics and the new variety, which I have called the Washington, gives promise of being heritably stable. It shows no tendency to either varietal or specific change, although growing under the same conditions which attend both the mutations which I have described and with which it originated.

There is nothing unusual in the physical conditions and environment of my garden. The soil is clayey, formerly part of a cultivated field, fertilized with stable manure and sodium nitrate, and watered with Potomac water. The seeds were germinated in window boxes, in garden soil, and transplanted on different ground for each year, soon after the spring frosts ceased. I do not know that any other case of mutation has ever occurred in the district which is occupied by the same soil and subject to the same environing conditions.

The new fruit compares favorably with the most approved varieties, and is therefore horticulturally valuable. But that fact is of little importance compared with the biological questions which arise concerning the mutative origin of the plant which bore it. I shall, therefore, in this article make no further reference to the fruit and discuss only the biological significance of the plant-mutation of which it was the joint product. The new variety, however, will be of botanical interest as a demonstration of the heritable character of varieties originating in correlation with specific mutation.

The sudden origination of new plant-forms having hitherto

been believed by many persons to be always due to hybridization, I refer to the following facts as proof that there was no cross-fertilization in either of the two cases mentioned, and that the new form is therefore not a hybrid. In neither of the two cases mentioned was any other variety of tomatoes grown with those which I planted, and no other grew in my neighborhood. Wind, or insect cross-fertilization was therefore quite improbable. Because I personally gathered, preserved and planted all my seed and cultivated all my plants, I am sure no substitution of either seed or plants occurred. The fact that in both those cases of mutation every plant of the whole crop partook equally of that act is itself proof that cross-fertilization did not occur. If my Acme plants had received adventitious pollination, or if pollen had reached them from any other flowers than those of their connate crop associates, the results of that cross-fertilization would necessarily have been incomplete as to the whole crop. It would also have been various as to the kinds of hybrids produced had the pollen come from more than one variety. Even if it were credible that the first case of complete mutation of the whole crop might have been the result of cross-fertilization from some unknown source, it would still be too much to believe that exactly the same result could have been produced a second time in successive years by such adventitious means. Therefore the question of hybridity is eliminated.

The origination of this new form was, in both instances, saltatory. It occurred in correlation with the ordinary function of intraspecific reproduction and was therefore accordant with both physiological and phylogenetic law. It did not result from cross-fertilization, and it is therefore assumed to have been a spontaneous result of some not yet ascertained exciting cause, and primarily due to some unknown determinate or predisposing cause.

After I had reached the foregoing conclusion as to the nature of the mutations which I had witnessed, public announcement was made of the publication of Professor de Vries' theory of mutation already referred to, and I at once began a comparison of his theory and observations with my observations which are described in the foregoing paragraphs. This comparison convinced me that my cases of mutation are similar in fundamental

character to those described by Professor de Vries, and the brief discussion I shall give them will be in accordance with that conviction. But to illustrate my remarks upon them it is necessary to briefly state the nature of his mutation theory and the methods he has pursued in demonstrating it; and also to show wherein it differs from the generally accepted Darwinian theory. For the sake of brevity these statements are mostly made in epigrammatic form. It is my purpose also, as far as possible, to present this brief sketch of the theory and its demonstration from the author's point of view, albeit in words of my personal choosing.*

The Darwinian theory of the origin of species by natural selection teaches that species have been produced from one another, through lines of genetic descent, by a process of evolutional variation which is immeasurably slow, even in its most accelerated cases; that one of the chief causes of specific change is the competitive struggle for existence to which all organisms are subjected; and that variation is incipient species-building. The enunciation of this theory was a strong and effective plea in favor of the origin of species by the operation of natural law as opposed to the then-prevailing belief that every organic form has arisen by a special act of creation. It has served a grand purpose, especially in establishing the doctrine of evolution on a firm basis, and if its candid and eminent author were now living he would be among the first to welcome any change in it that might prove to be necessary in view of later discovered facts.

The de Vriesian theory of mutation is in entire accord with natural law and also with the doctrine of the evolutional origin of species through lines of genetic descent, but it especially makes a clear distinction between species and varieties and teaches the sudden origination of the former whether they possess more or less strongly marked attributes. It also teaches a far more stable entity of species than one can conceive of who unqualifiedly accepts the Darwinian theory. Professor de Vries logically assumes that the mutation theory is as applicable to animals as to plants, but he has formulated it only with reference to the latter. I shall make

* A somewhat fuller, but brief, statement of the mutation theory is given by me in the Annual Report of the Smithsonian Institution for 1901. An interesting general sketch of the theory by Professor de Vries is contained in Science for May 9, 1902.

only a similar reference to the theory in following paragraphs, although my former paleontological work suggests a much wider application of it.

The theory begins with a philosophical concept concerning the molecular constitution of the protoplasm of organisms, as set forth in the author's treatise on intracellular pangenesis.* It assumes that the specific attributes of multicellular plants result from the special molecular constitution of their protoplasts, or cell contents; and that these attributes are built up of sharply defined intracellular units, which normally combine in groups. This specific group-combination has much stability, but it is subject to change by sudden, independent action of some unknown determinate cause. That change is the initial step in mutation and consists of the addition, or substitution, of one or more units to an established group and the consequent rearrangement of the units of that group, forming a new one.

Upon the integrity of the groups of units depends the stability of the specific attributes. Their normal tendency to stability is so great that initial group-changes do not occur in the somatoplasts of plants but only in the plasma of certain of their reproductive cells; and they occur there only seldom. Ordinarily, when such a change occurs, it is only in the oöplast of the germ cell of the ovule which is about to originate a new plant. If no change of specific units occurs in the oöplast the case is one of ordinary reproduction. If such a change does occur in the oöplast the case is one of mutation as well as of reproduction, all the cells of the coming plant naturally partaking of the same specific attributes.

It should be here remarked that such cases as the reputed origination of the nectarine from the peach are apparent exceptions to the rule just mentioned. That case being one of ordinary asexual reproduction and if it really was also a case of simultaneous origination of a new species, initial mutative change must have occurred in the plasma of the apical cell of the mutating bud. If mutation may occur in correlation with asexual reproduction, mutative molecular change in pollen cells would seem to be unnecessary in mutating cases of sexual reproduction.

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* See Intracellulare Pangenesis. Von Hugo de Vries. Pp. 212, Jena, 1889.

Mutation is, therefore, the saltatory origination of new organic species resulting from sudden molecular change in their initial protoplasts. The new species is at once such, without preliminary preparation, without intermediary gradation, and without any subsequent addition of attributes. Newly mutated species differ clearly and distinctly, but not widely, from the parent species. Wide differences between species of a genus indicate the death of intervening species. As a rule, mutation occurs, not by, or in connection with cross-fertilization, but in correlation with pure intraspecific sexual reproduction, and nevertheless independently of it. A new and stable specific form is thus produced, but the parent species remains intact. Mutation is, therefore, a strictly phylogenetic process, although plural cases occurring in one and the same mutating species are often randomly divergent in character.

Hybridization occurs in nature, and very often in cultivation, but it is not mutation. Neither is it really phylogenetic in character, but a result of ontogenal miscegenesis, with the groups of molecular specific units unbroken in each parent germinal portion. According to Mendel's law, even fertile hybrids are sooner or later obliterated by the prepotency of one or the other of the parent forms.

Mutation, being a normal process, does not produce monstrosities. The latter are cases of distorted or abnormal ontogeny.

Above all, variation is not mutation, nor are varieties incipient species. Ordinary fluctuating, or individual, variation is an inseparable accompaniment of all plants, and racial variation also widely prevails, but no kind of variation leads to mutation proper.

Mutation, being a result of intracellular molecular change, is necessarily sudden, as is molecular substitution in chemical reaction. One cannot concieve that molecular change could continue in action toward one result through immeasurable time. A species being suddenly produced implies that its normal state is one of at least a considerable degree of stability.

Species being normally stable and only incidentally mutable, a part of the time-existence of each is therefore a mutative, and a part an immutative, period. The immutative period is, as a rule, so very much longer than the mutative period that very few mutable plants exist simultaneously in any flora. Because of these

facts, of the great prevalence of fluctuating varieties, and for other reasons, mutation has hitherto usually escaped observation, even by naturalists.

When a new species originates by mutation in the wild state it is at once subject to the usual competitive struggle for existence, even with its parent form. Species not only do not originate by natural selection and the struggle for existence, but they perish thereby; and the number of species which have originated by mutation since the beginning and met an untimely death without having produced any progeny, is doubtless beyond human estimate.

Acting upon the theory which is very briefly stated in the foregoing paragraphs, Professor de Vries formed a systematic plan for discovering and studying mutating plants. He selected from the flora of Holland more than one hundred species and transplanted them in experimental gardens at Amsterdam, where he also sowed seed of those, and many other members of the Holland flora. He also made exhaustive studies of that flora in its wild state. The object of these experiments was not to produce horticultural varieties but to discover plants that were already in their natural mutative period among the multitude that were plainly immutative. He nurtured, protected and artificially pollinated the plants thus growing under his care. In short, he fully supplied their natural wants, gave them much greater advantages of growth and development than the best wild conditions could afford, and relieved them from all the adverse conditions which they necessarily would have encountered in their wild habitat. Meanwhile he eagerly watched them all for any sign of mutation that might occur.

The result was at least one grand success amid a multitude of failures. The failures were not due to the method of investigation, but to the fact that almost all the plants investigated were in their immutative period. The chief case of success was with plants of the American genus *Oenothera*, the so-called evening primroses. One species, *O. Lamarckiana*, proved to be in an exceptionally mutable condition. A few years ago it escaped from cultivation in certain parks in Holland and immediately began a most vigorous multiplication and dispersion in a wild state. Among the abundant original plants thus produced, two new species soon ap-

peared which Professor de Vries believed had originated then and there by mutation from *O. Lamarckiana*. He transferred many of those plants and much of their seed to his experimental gardens and there verified that belief by obtaining a repetition of those two mutations under his direct observation. Furthermore, in the course of a few years of experimentation, he obtained by mutation from *O. Lamarckiana* five other new species, seven in all. A part of these new species proved to be also mutative, adding still other new ones to his list; and all the new ones possessed, from the moment of their origin, well-defined and heritable attributes. These mutations occurred in the progeny of plants which had received intraspecific artificial pollination. Interspecific pollination, or cross-fertilization, was not found to facilitate mutation, and hybridization was not sought for or desired.

In view of the success of Professor de Vries' experiments with *Oenothera*, and the fact that all except one or two per cent. of the species with which he experimented failed to show any sign of mutation; and the further fact that he experimented with only a part of the Holland flora, one infers that the proportion of immutative plants to the mutative may perhaps be as great throughout the plant kingdom as he found it to be in that flora.

Recognizing the fundamental accordance of my observations with those of Professor de Vries, I assume that *Lycopersicum* is, like *Oenothera*, in its mutative period and that *L. esculentum* has given mutative origin to two other species which, in previous paragraphs, I provisionally designated as groups. The fact that these two specific forms differ less from each other, and from their common parent *L. esculentum*, than do some other species from one another, does not affect the validity of the claim that they should also be regarded as distinct species. The facility with which all forms of *Lycopersicum* hybridize with one another also does not affect that claim because of the non-phylogenetic character of hybridization. I shall therefore apply the systematic name of *Lycopersicum solanopsis* to the solanoid group, and the latifoliate group accordingly becomes *L. latifoliatum*; but the atavic group must retain its original name of *L. esculentum*.

While the cases of mutation which I have observed in *L. esculentum*, fundamentally accord with those which Professor de

Vries observed in *Oenothera Lamarckiana*, they present some peculiar features, the chief of which are shown by the following comparisons. In none of his cases do specific attributes seem to have been complicated with varietal characters, unless one should except the case of *O. nanella*. Perhaps a sufficient reason therefor is that most of the species of *Oenothera* have hitherto shown very little tendency toward variation. On the contrary, *Lycopersicum solanopsis* became divided into several varieties soon after its first mutation from *L. esculentum*. I do not know in what variety it first appeared, but in the first of the two subsequent mutations, those which I observed, it appeared in a new variety, the Washington. Furthermore, in the next mutation, which was quite independent of the others, it appeared in the same variety. Indeed, in all the cases of specific mutation of *Lycopersicum* to which I have referred, some one horticultural variety seems to have been a conjunctive vehicle for the introduction of the new species.

The scope of mutative action in *Oenothera* has been given in detail by Professor de Vries, but my observations show that in *Lycopersicum* the scope of that action is different in certain respects. He found mutation in *Oenothera* to act independently and separately upon the germ of each one of a very small number of seeds in an abundant fruitage of a large crop of plants; and that those seeds were usually subject, not to one and the same mutation, but to different specific mutations. I found in *Lycopersicum* that one specific mutation acted completely and uniformly upon the germs of all the seeds, of all the fruits, of every plant of my crop of 1899, and that it acted in precisely the same manner in the crop of 1901. The suddenness of its action in the latter crop especially, is shown by the fact that the Pennsylvania Acme seeds, planted in my garden in 1900, gave a full and uniform crop of true Acme plants; and that it was their seed which mutated so completely upon the same ground in 1901. In view of my repeated experience with the Acme variety one seems to be justified in assuming that the determinate cause of mutation is now latent in every plant of that variety wherever grown, and that it quickly manifests itself when the flowering plants are brought under the influence of a favorable, exciting cause.

Again, Professor de Vries found that some of his newly mutated species of *Oenothera* were themselves immediately mutable. My observations of the mutation from *Lycopersicum esculentum* to *L. solanopsis* seem to indicate that the mutative act was coincident with impending varietal senility in the Acme variety, and that the resulting variety, the Washington, has no tendency to mutate. Doubtless *L. esculentum* originated by mutation from some other pecific form of that genus, but no evidence seems to be obtainables that, although variable, it began to be really mutable until many years after the species became horticulturally known. These facts indicate that in some species the mutative period occurs in one part of their time-existence, and that in other species it occurs in another part of the same.

Some of the observations made by myself in the cases of mutation of *Lycopersicum* are thus seen to be different from any of those made by Professor de Vries in cases of mutation of *Oenothera;* but the facts which we have both observed are not in conflict. Their differences only indicate that the field of investigation which that distinguished botanist has opened in close contact with nature is a very broad one.

SMITHSONIAN INSTITUTION, 15 July, 1902.

New Western Plants

By Alice Eastwood

I. NEW SPECIES FROM COLORADO AND UTAH

Castilleia scabrida

Stems low, 5–10 cm. high, from a perennial root, leafy, flowering from near the base or half way to the top. Entire plant canescent with a stiff scabrous and hispid pubescence: lower leaves linear-oblong, obtuse, 1–2 cm. long, 2–3 mm. wide, the midrib prominent; upper leaves 3–5-cleft, with spreading divisions, the lower part broad, 3-ribbed; bracts similar to the upper leaves, colored: calyx obliquely gibbous at base, 2.5 cm. long, about equally cleft, hispid especially on the nerves; divisions linear, 6–7 mm. long: corolla with half the galea extending beyond the calyx lobes: lower lip protuberant with acuminate divisions: stamens and style exserted, the latter surpassing the former: capsule ovate-acuminate, 15 mm. long, 8 mm. wide, distending the calyx as it ripens: seeds brown, shining as if varnished, linear-oblong to clavate, scrobiculate.

This was collected at Grand Junction by Mrs. H. C. Long in the spring of 1890. The type is in the herbarium of the California Academy of Sciences.

Lappula gracilenta

Stems erect, 4–6 dm. in height, branching from the base or half way up with slender, spreading branches, hispid throughout with white hairs which are horizontally spreading on the stems and margins of the leaves, appressed on the surfaces of the leaves and calyx, wanting on the corolla: leaves crowded at base, spatulate to oblanceolate, narrowed to a margined petiole of about the same length as the blade, together 2–8 cm. long, about 1 cm. wide, the earliest leaves shorter and broader in proportion: cauline leaves lanceolate, sessile, 6 cm. long, 1 cm. wide, becoming smaller as they ascend, entire or obscurely denticulate along the upper margin: internodes not quite equalling the lower leaves, surpassing the upper ones: bracts generally alternating with the flowers, becoming smaller and linear on the upper part of the racemes: pedicels slender, recurved in fruit: divisions of the calyx extending almost to the base, linear, obtuse, 2–3 mm. long, spreading under the nutlets: corolla blue, with white folds in the throat: divisions obovate,

4 mm. long, 3 mm. wide, twice as long as the short tube: folds in the throat thick, each of 3 wart-like crests, the middle one largest: stamens on short filaments which are concealed by the large anthers, 1 mm. long, inserted below the folds and alternating with them: scales at the base of the corolla tube fleshy, in pairs: style short: stigma capitate: nutlets ovate, 3 mm. long, 2 mm. broad, the surface pubescent and having a few barbed bristles which are .5–2.5 mm. long, generally a long and short one alternating.

This beautiful species grows in the cañons of Mesa Verde in southwestern Colorado where the cliff dwellings are situated. The type specimens were collected by the author in Navajo Cañon, June 7, 1892.

Type in the herbarium of California Academy of Sciences.

Corydalis Wetherillii

Annual or biennial, branched from the base and also above, with slender, erect stems and branches, 10–15 cm. high, glabrous and glaucous: leaves dissected, the lower on long slender petioles, twice-compound with 5 primary divisions on capillary petiolules, secondary divisions fan-shaped, 3–5-parted with ultimate divisions spatulate, entire, or 3-lobed, acute, minute: peduncles axillary from near the base to the top of the stems, 1 mm.–2 cm. long, with 1–3 flowers at summit as well as some abortive ones: bracts linear-acuminute, entire or with a few teeth near the summit: sepals 2, membranous, triangular, scale-like, less than 1 mm. long: corolla 2 cm. long, the spur rounded at base, straight, 4 mm. long: outer petals pinkish, hooded but without dorsal crests: inner yellowish, as long as the outer, with wing-like crests on the back: capsules linear or linear-lanceolate, straight or somewhat curved, 2 cm. long, tipped with the persistent style and disk-like stigma: seeds flattened, orbicular, black, very glossy, 2 mm. in diameter, faintly marked under a 10-diameter lens with a fine quadrangular venation.

This peculiar species was collected near Bright Angel Creek, one of the branches of the Colorado River which comes into the river nearly opposite Hans' Trail. This trail is that taken by tourists who go into the cañon from the Flagstaff side. It is named in honor of Mr. Alfred Wetherill who collected it in the summer of 1897.

The foliage is more finely dissected than in any other species known to me. It is perhaps more nearly related to the group which contains *C. aurea* but it is quite distinct from that or any other known species. The type is in the herbarium of the California Academy of Sciences.

II. TWO NEW SPECIES OF CAMPANULA FROM THE PACIFIC COAST

Campanula stylocampa

Stems slender, erect, about 2 dm. high, simple, purplish, ribbed with scabrous angles, otherwise glabrous. Leaves alternate, oblanceolate to linear, acuminate, 2–3 cm. long, becoming smaller as they ascend, tapering to a sessile base, veinless except for the midrib, revolute and crisped-undulate along the margins, the lowest leaves ciliate at base: flowers solitary, terminating the stems: calyx with narrow, linear-subulate divisions, 8 mm. long, .5 mm. wide, glabrous, revolute and somewhat undulate at base: corolla divided almost to the base; divisions lanceolate, 13 mm. long, 4 mm. wide at base, with cucullate apex and undulate margin: anthers linear, 7 mm. long, on short, narrowly linear filaments 2 mm. long, abruptly widening to an orbicular base, 2 mm. wide, hairy along the margin: ovary urceolate, ribbed, opening under the calyx: style long, exserted, 12 mm., erect at base, then curved like a sickle downwards, 3-cleft at apex when developed: fruit not present.

This unique species of *Campanula* was collected by George Fenwick near Dawson, N. W. Territory, in the summer of 1900.

The specific name arises from the peculiarly curved style in which it differs from all other species of North American Campanulae. Type in the herbarium of California Academy of Sciences.

Campanula Baileyi

Stems from creeping, filiform rootstocks, 6–12 cm. high, slender, simple, erect, glabrous, angled or ribbed, leafy up to the solitary, terminal peduncle. Lowest leaves cuneate or obovate, toothed along the apex, middle stem leaves elliptical-lanceolate, sharply serrate with a few teeth; upper ones more distant, narrowly lanceolate or entire: peduncles at first nodding, becoming erect, about 2.5 cm. long: divisions of the calyx triangular-subulate, acuminate, 1 cm. long, glabrous: corolla blue, 14 mm. long, with divisions 8 mm. long, linear-lanceolate, minutely cucullate at the apex: anthers 6 mm. long, linear, mucronate: filaments broadening from 1 mm., as wide as the anthers, to 2 mm.: style not exserted, as long as the stamens: ovary turbinate, opening just below the divisions of the calyx: fruit not seen.

This was collected by Mr. Vernon Bailey, in the mountains at the head of Canyon Creek, Trinity county, California, August, 1899.

While it is distinct from all other species of *Campanula* it probably comes nearest to *C. linnaeifolia* Gray. Type in the herbarium of California Academy of Sciences.

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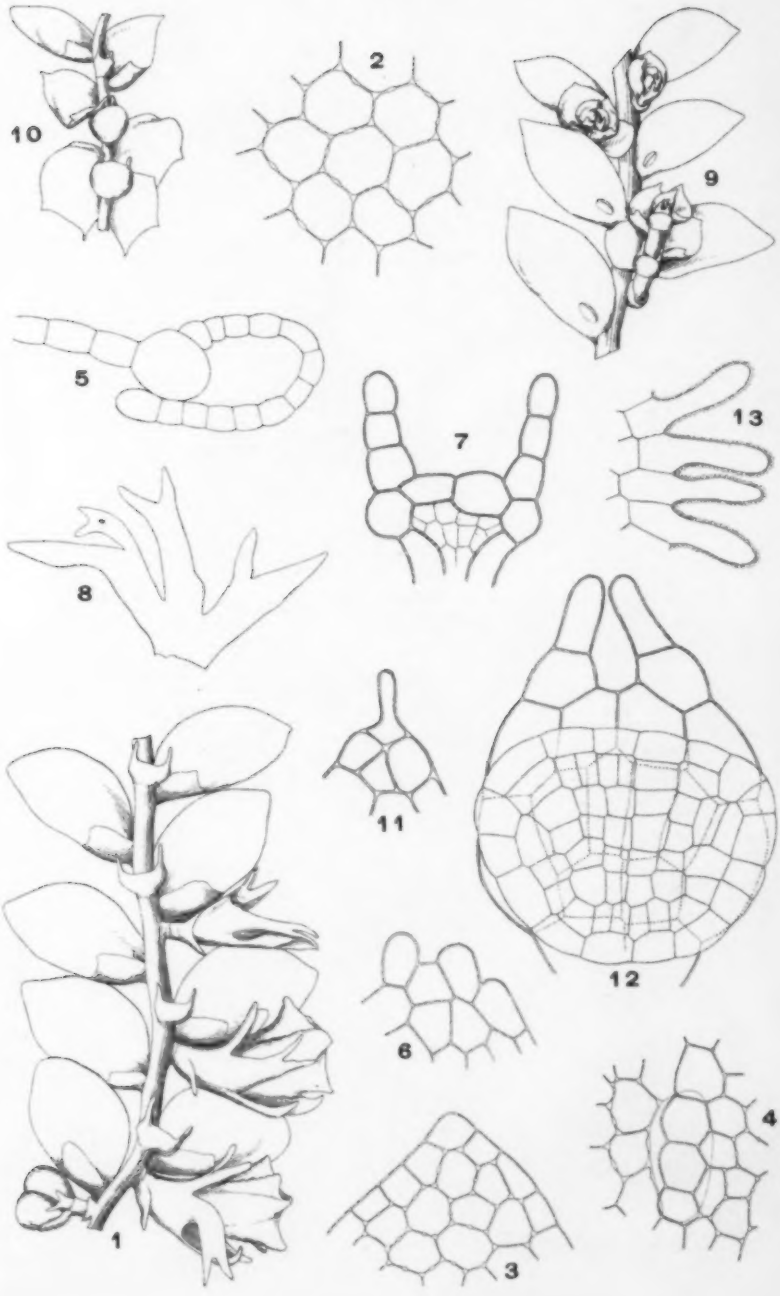
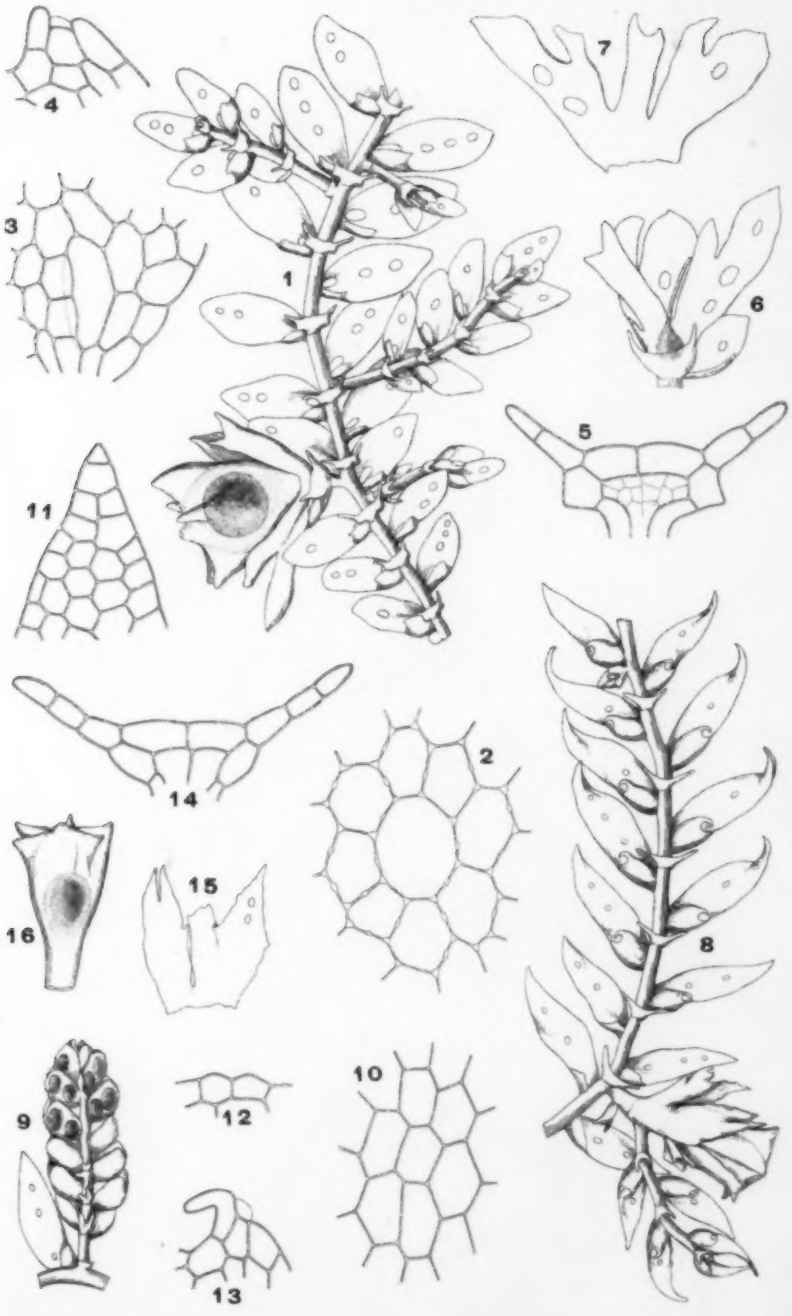
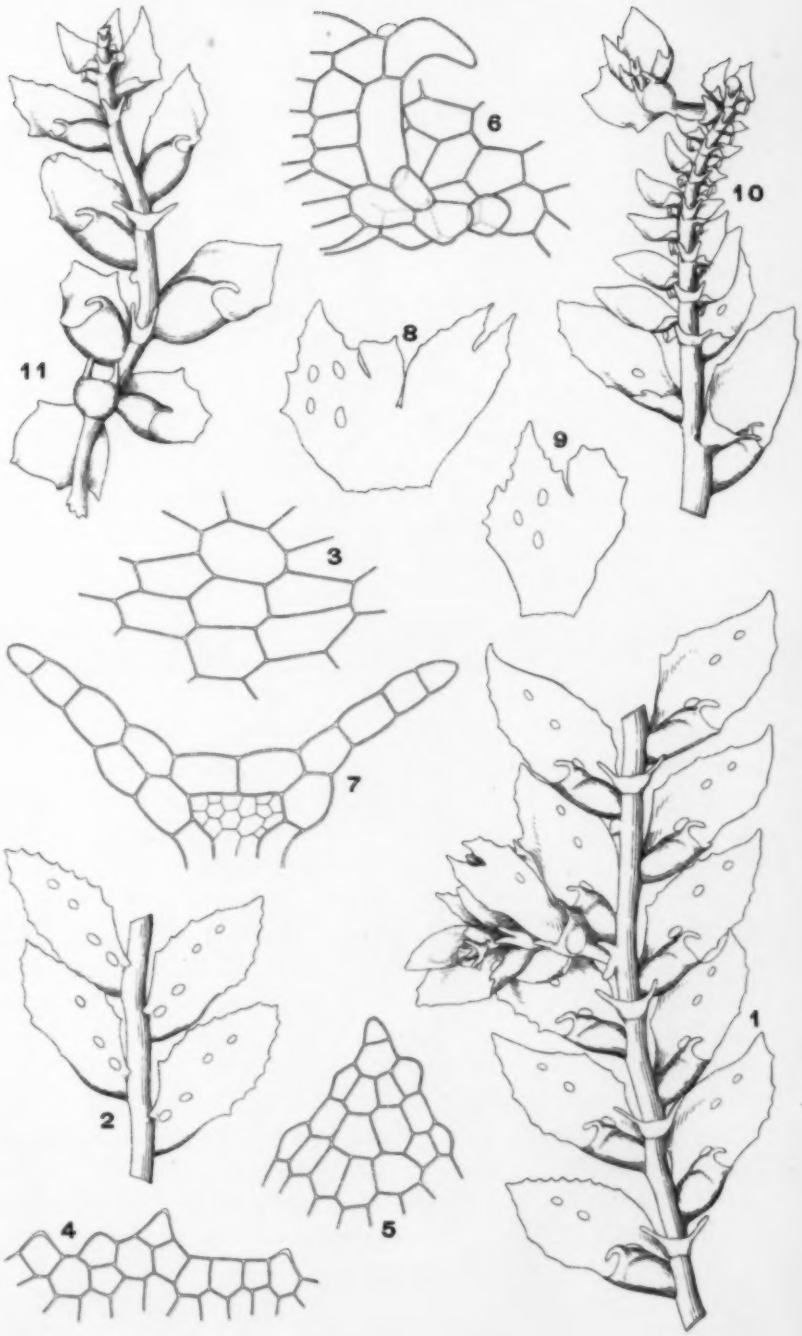


LEPTOLEJEUNEA EXOCELLATA (Spruce) Evans.



LEPTOLEJEUNEA ELLIPTICA (Lehm. & Lindenb.) Schiffn.
LEPTOLEJEUNEA STENOPHYLLA (Lindenb. & Gottsche) Schiffn.

HELIOTYPE CO., BOSTON



LEPTOLEJEUNEA HAMULATA (Gottsche) Schiffn.